PLATE XVI. *Webera camptotrachela.*—*a*, entire plant; *b b*, leaves; *c*, areolation of the middle; *d d*, external perichætial leaves; *e*, inner perichætial leaf; *f*, capsule with the lid; *g g*, capsule deoperculate; *h* portion of the external peristome; *i*, portion of the inner peristome.

PLATE XVII. *Polytrichum Ohioense*, compared with P. formosum, P. gracile and P. commune.—*a*, transverse section of the lamellæ of the leaves of P. Ohioense; *b*, ditto of P. formosum; *c*, ditto of P. gracile; *d*, ditto of P. commune; *e e*, capsule of P. Ohioense; *f*, capsule of P. formosum.

PLATE XVIII. *Fontinalis Howellii.*—*a*, entire plant; *b b*, upper stem-leaves; *c c*, branch-leaves; *d*, perichætial leaf; *e*, capsule; *f*, portion of the external peristome; *g*, portion of the lattice cone.

PLATE XIX. *Fontinalis flaccida.*—*a a*, leaves; *b b*, point of same; *c*, areolation of an auricle; *d*, areolation of the middle.

PLATE XX. *Camptothecium Amesiæ.*—*a*, entire plant; *b*, branch-leaf; *c*, areolation of the base of same; *d*, perichætial leaves; *e e*, capsule with pedicel; *f*, portion of the outer and inner peristome.

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## Zygomorphy and its causes. II.

CHARLES ROBERTSON.

As soon as a shallow flower becomes horizontal the insect relations change, and certain modifications which would be corrected in vertical flowers become advantageous. While the flower is erect, the horizontal petals form a convenient landing. When the flower turns to one side, the petals become vertical, and the stamens and styles, which become horizontal, form the landing. The flower immediately becomes sternotribe, and this shows how an apparently trivial variation may be of great functional importance. The pollen, instead of being scattered indefinitely on all sides of the insect, is now limited to the under side. It will be advantageous for the stamens and styles to bend so as to strike the ventral surface of the bee with more precision.

The upper nectary, being in front of the landing, is most convenient, and is first to be sucked. To suck the lower nectaries, the bee must turn and hang under the stamens, a very inconvenient operation which causes delay. This view and, in fact, the whole theory stated in this paper was suggested by the action of a bee, *Synhalonia speciosa* Cress.,[12] on the flowers of Geranium maculatum.

The flowers are terminal and vertical, or nearly so, and insects light upon the petals. Humble-bees, which seem best adapted to fertilize the flower, pull it down by their weight so as to invert it, as observed by Prof. Macloskie.[13]

[12] The bees mentioned in this paper were named by Mr. E. T. Cresson.
[13] BOT. GAZ. IX, 157.

Smaller visitors do not bend the peduncles. The Synhalonia bent them so that the stamens and styles turned to an horizontal position. To keep her body upright, the bee took a position on the upper side of these, and sucked only the upper nectary. When she visited a few flowers which were bent to one side, she lighted on the stamens and sucked the upper nectary. Only once did she insert her proboscis into all of the nectaries, and then with difficulty, since she had to turn upside down and hang to the stamens.

The very fact that a bee lighting on the stamens sucks the upper nectary first must have a serious influence on the lower ones. Since bees are often disturbed before they have emptied all of the nectaries, the one which is most convenient is most likely to be sucked. Darwin has observed[14] that "when flowers having more than a single nectary are visited by many bees, so that the nectar is exhausted in most of them, the bees which afterward visit such flowers insert their proboscides only into one of the nectaries, and if they find this exhausted they instantly pass to another flower." Now, suppose a bee neglects the lower nectaries from being disturbed, or, like the Synhalonia, because it objects to reversing, the next bee trying the upper nectary and finding it empty will come to the erroneous conclusion that the lower also are empty, and may neglect them on that account.

The first change toward zygomorphy is for the stamens and styles to turn down at the bases and up at the tips, so as to strike the ventral surface of the bee more effectually, and this is an additional cause of the abortion of the lower nectaries, by rendering them less accessible.

Hibiscus lasiocarpus[15] is a good example of a flower in the first stage of irregularity. When the flower is open, insects light on the base of the staminal column. The free ends of the filaments are directed from the upper and lateral portions of the column, so as to dust the ventral surface of the bee which lights upon them. The styles are bent upward, holding the five capitate stigmas in such a position that bees strike them before they land. After sucking, the bees crawl out over the filaments and upon the lower petals, leaving the flower without again touching the stigmas.

Most of the flowers are as in fig. 1, one nectary (3) is

[14] Orchids, 42.

[15] The flower is adapted to larger bees, Apidæ, of which I have found the following: *Bombus separatus* Cress. (f), *B. Pennsylvanicus* De Geer. (n), *Apathus elatus* Fabr. (m), *Melissodes bimaculata* St. Farg. (m), *Emphor bombiformis* Cress. (mf), *Megachile brevis* Say (m).

uppermost, and the column is bent down, so as to come between 1 and 5.

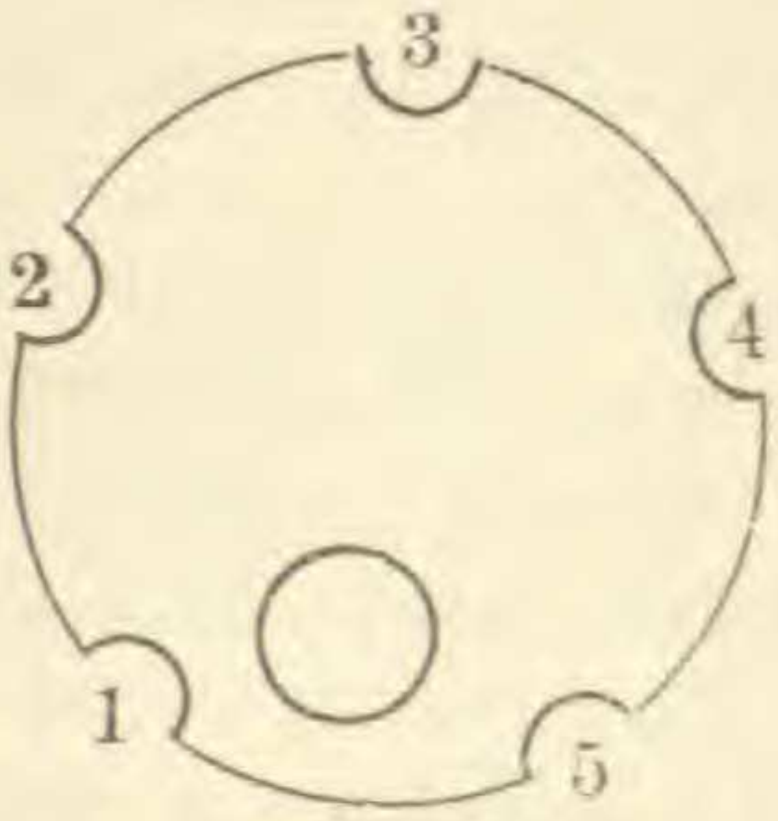


Fig. 1.

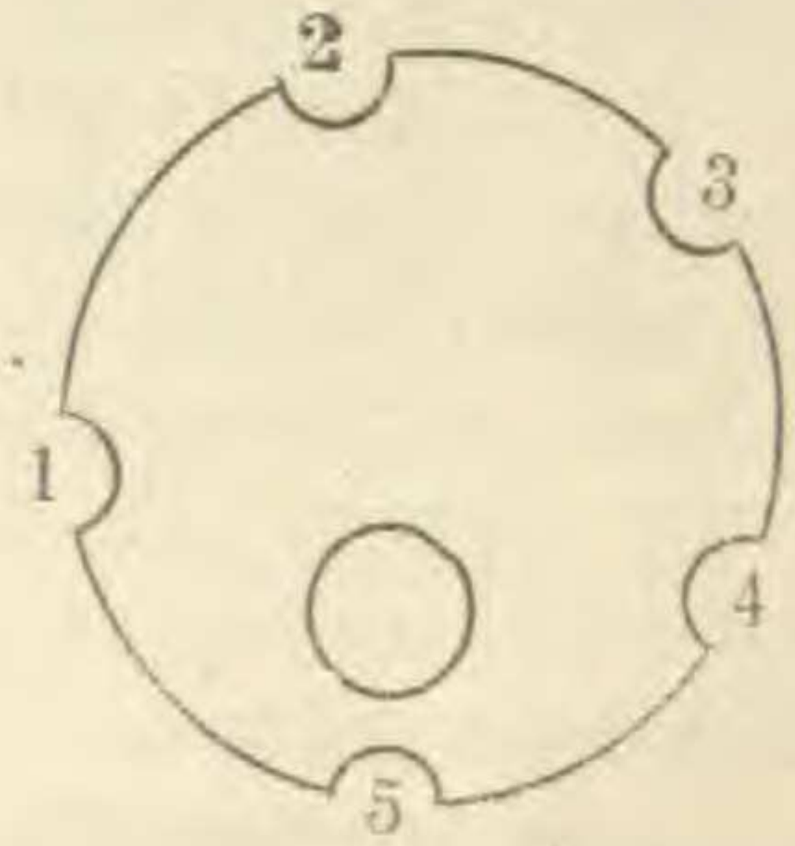


Fig. 2.

Emphor bombiformis is by far the most abundant visitor. Indeed, in two seasons' collecting of insects on flowers, I have failed to find this bee except on this plant. The female visits the flower for honey and pollen, her loose scopa being well adapted to hold the large grains. The male comes for honey and in search of the female. In sucking, this bee generally begins with 4 and turns to the left, often missing 5, but sometimes reversing, so as to empty all. Of 27 individuals, only 10 sucked 5 nectaries, 17 missing one or more. The 27 sucked 113 out of a possible 135 and missed 22.

Bombus Pennsylvanicus, which is next in abundance to the Emphor, generally begins with 2 and sucks to the right, rarely reversing, so that it usually misses 1. It often misses 5, also, especially when this nectary is under the column, as in fig. 2. Of 56 individuals, only six sucked 5 nectaries, 50 missing one or more. The 56 sucked 195 out of a possible 280 and missed 85.

Compared with Emphor bombiformis, Bombus Pennsylvanicus misses the lesser nectaries more frequently. The Emphor, therefore, has more influence in preserving the regularity of the flower. Now, if this bee becomes less frequent on account of competition with the more diligent humble-bee, or from any other cause, the irregularity of the Hibiscus will be hastened.

The lower nectaries, being commonly neglected, are most likely to contain nectar; yet, if a bee finds no nectar in the first or second of the upper ones, it leaves the flower as if inferring that the lower are empty.

As stated above, Bombus Pennsylvanicus does not turn back, but sometimes sucks the fifth nectary (no. 1 in fig. 1) by squeezing under the column. This causes considerable delay, which is a disadvantage both to bee and flower. We can see, therefore, how an abortion of the lower nectaries would be advantageous.

In the insect relations of this flower we find the conditions which have given rise to more complicated forms, and which may still further modify the Hibiscus.

When a flower with a single central nectary becomes horizontal, its new position makes access to the nectary useless, except on the upper side, and this makes possible different modifications of the lower parts, which make the nectar inaccessible except above. In many Papilionaceæ, for example, nine lower stamens are united, leaving a way to the nectar only on the upper side.

When the flower turns to an horizontal position, the effect on the petals is to deprive them of their function as a landing, and this makes possible many specializations for other purposes.

The upper petals remain expanded, so as not to come in the way of an insect lighting on the stamens and styles. Since an insect about to alight approaches the flower from above and in front, the upper petals are more conspicuous than the lower, which are hidden by the reproductive organs. The upper petals, therefore, retain their attractive function, while the lower lose this office, also, as well as that of a landing, so that the advertisement is retained on the upper side of the flower. In Papilionaceæ the upper petal is much enlarged, forming the vexillum. Irregular flowers of shallow origin, in general, have the upper petals larger and brighter colored.

Since the lower petals are deprived of their function both as organs of attraction and as a place of landing, and since access to the nectaries is no longer important on the lower side, these petals are free to assume any position and undergo any amount of modification which will fit them for a new function. In Gaura[16] they have turned so as to help the upper petals in attracting visitors. Often they become less expanded, aiding the stamens and styles as part of the landing. In Papilionaceæ two lower petals are united, forming a lighting-place for insects, increasing the attractiveness of the flower, protecting the stamens from rain and from pollen-eating intruders, and enabling them to strike the visitor with more precision[17].

[16] For illustration of Gaura Lindheimeri, see Wild Flowers of Am., pl. XXIII.

[17] While most Papilionaceæ are sternotribe, and all were no doubt originally so, in Phaseolus the keel guides the stamens against the insect's side, making the flower pleurotribe. In Apios the tip of the keel is fixed to the summit of the banner, and when dislodged must strike the insect's back, making the flower nototribe.

If the above observations indicate the conditions which have given rise to sternotribe flowers, irregular polypetalous flowers would be expected to be sternotribe, and this is the rule with them, as far as I know. Examples are: Delphinium, Aconitum (Ranunculaceæ), Hibiscus lasiocarpus (Malvaceæ), Pelargonium (Geraniaceæ), Æsculus (Sapindaceæ), Polygala (Polygalaceæ), Papilionaceæ, Gaura (Onagraceæ), Rhexia (Melastomaceæ), Cuphea viscosissima (Lythraceæ). Also, Hemerocallis, Pontederia, etc., among Monocotyledons.

Some of these flowers show no indications of the conditions which are supposed to have produced them. Thus, Trifolium pratense is no longer shallow, but is deep and tubular, the insect no longer lighting on the flower, but on the head, and the pollen is dusted on the under side of the bee's head or proboscis. My theory only requires what would be supposed from its affinities, viz., that the flowers were originally polypetalous and have become smaller and crowded. It not only follows from my theory that these flowers must have been visited separately by bees lighting on the stamens, but, as already observed, there are reasons for claiming that originally small, regular lateral flowers in close clusters would not be rendered irregular by insects. Moreover, the effect of insects visiting such flowers is so far from tending to make them irregular that it tends rather to turn such irregular flowers back to a more regular form; for, unless the organs are protected by a rigid galea or keel, the flowers will be fertilized by insects brushing over them, instead of applying pollen to the upper or under side of the insects. The flowers of Trifolium are protected, but Amorpha seems to have lost its papilionaceous character in this way. It has lost wings and keel, only retaining the vexillum, which makes the spikes more conspicuous, and its insect relations are much the same as in the apetalous Salix.

But there are some flowers of polypetalous origin which are nototribe, such as most orchids, Impatiens and Viola (sometimes).

The orchids must have been developed as sternotribe, and become nototribe by the twist in the ovary, which inverts the flower. The labellum must have been developed as an organ of attraction, like the vexillum of Papilionaceæ and the upper colored sepals of Pontederia, and has become a landing on account of the flower turning upside down. It is remarkable that these flowers, whose structure required them to become sternotribe, should finally become the highest specialized of nototribe flowers, far outstripping those which became nototribe more readily, and assuming adaptations which aim at all parts of the upper sides of insects. Thus, Orchis pyramidalis[18] fastens its pollinia on the upper side of the proboscides of Lepidoptera; O. spectabilis fastens them on the smooth part of the face of female humble-bees; Habenaria orbiculata, on the eyes of Sphingidæ;[19] Calopogon parviflorus, on the first segment of the abdomen of small bees;[20] the Calopogon seems to have gone through some remarkable changes. From being regular and dusting pollen indefinitely on the visitor, it first changed so as to dust the ventral surface. Then, inverting, it fastened the pollen on the upper side of the bee. Then it turned right side up again; but it has not, however, become again sternotribe, but remains the most remarkable of nototribe flowers. It has quit turning upside down to strike the insect's back. It turns the insect upside down to strike its stigma. As far as I know, Calopogon is the only nototribe flower of shallow origin which is not inverted.

Another nototribe flower, which is polypetalous, is Impatiens—at least, some of the species. They must have become sternotribe and then become inverted by becoming pendulous.[21]

*Carlinville, Ill.*

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## Some notes on Western Umbelliferæ. III.

JOHN M. COULTER AND J. N. ROSE.

**Peucedanum Austinæ**, n. sp. Resembling P. Hallii, but with leaf-segments larger and pinnate with narrow often toothed divisions; flowers purplish; fruit as in P. Hallii ($3\frac{1}{2}$ lines long, $1\frac{1}{2}$ lines broad), except oil-tubes solitary in the dorsal intervals, mostly 2 in the laterals, 4 on the commissural side, and an additional one in each group of strengthening cells: seed-face concave, with central longitudinal ridge.—California. Plumas county (*Mrs. R. M. Austin*, June, 1880); near Yreka (*Greene* 732). Distributed as *P. Hallii* Watson.

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18 Darwin, "Fertilization of Orchids," 16.

19 Gray's "Structural Botany," figs. 466 and 466a.

20 BOT. GAZETTE XII, 288.

21 Flores pedicello debili fulti, sæpius propter pondus calcaris invertunter, et calcar, reversa posticum, anticum apparet. Benth. & Hook. Gen. Plantarum, I, 277, Impatiens.